Vol. 111. Pt. 12. Pp. 351–364. 7 figs. 11th December, 1959.

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ROYAL ENTOMOLOGICAL SOCIETY

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World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGE

WAY, M. J. The effect of temperature, particularly during diapause, on the development of the egg of *Leptohylemyia coarctata* Fallén (DIPTERA: MUSCIDAE) . . . . . 351–364. 7 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 6s. 0d.

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THE EFFECT OF TEMPERATURE, PARTICULARLY DURING DIAPAUSE, ON THE DEVELOPMENT OF THE EGG OF *LEPTOHYLEMYIA COARCTATA* FALLÉN (DIPTERA: MUSCIDAE)

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Manuscript received 1st April, 1959

(Read 6th May, 1959)

With 7 Text-figures

Contents

I. Introduction 351
II. Methods 352
III. Egg development in natural conditions 353
IV. Egg development at controlled temperatures 355
V. Optimum constant temperature for diapause development . . 357
VI. Development before and after diapause. 360
VII. Development at constant temperatures 361
VIII. Discussion 362
IX. Summary 363
X. Acknowledgments 363
XI. References 363

I. Introduction

Diapause in insects ends only after a period of physiological development during which there is little or no morphological change (Andrewartha, 1952) and for which the temperature needed is nearly always lower than for morphogenesis. Details of temperature requirements for diapause development are known for some insects (Andrewartha, 1943; Hodson and Weinman, 1945; Danilyevsky, 1949; Muroga, 1951; Browning, 1952; Lees, 1953; Williams, 1956; Schneiderman and Horwitz, 1958). Danilyevsky (1949) and Lees (1955) demonstrated the close relationship between the temperature requirements for ending diapause and the temperatures the diapausing insect normally experiences. Thus, about 10–20°C. is needed for species of sub-tropical regions, in contrast to 0–10°C. for those of temperate regions. Even lower temperatures suit some species normally subjected to severe cold; diapause development can occur at −5°C. in eggs of *Malacosoma disstria* Hübner (Hodson and Weinman, 1945), at −10°C. in larvae of *Gilpinia polytoma* Hartig (Prebble, 1941) and at −15°C. in pupae of *Saturnia pavonia* L. (Danilyevsky, 1949).

This paper shows how the development of the egg of *Leptohylemyia coarctata* Fallén is affected by temperatures, most of which are within the range it would

normally experience. The action of very low temperatures is described separately (Way, *in press*).

The eggs are laid during the hottest time of the year (late July to August) and hatch at about the coldest time (end of January to early March). The favourite site for egg laying is bare soil, so that eggs remaining close to the soil surface experience a big diurnal, as well as seasonal, temperature variation. There is one generation a year and diapause is apparently obligatory.

II. Methods

Adults of *L. coarctata* were caught in the field and kept in a constant temperature room at 20°C. in specially devised breeding cages (Bardner & Kenten, 1957). The eggs were usually collected twice daily and were kept in batches of 10–20 between two $1\frac{1}{2}$-inch diameter circles of parachute nylon, either at a depth of about 1 inch in moist sterilised potting soil in flower pots, or on a pad of moist cotton wool in 2-inch × 1-inch corked specimen tubes. The soil method was used in outdoor experiments and in experiments where the eggs were kept for a long time at relatively high temperatures. Otherwise, they were kept in tubes. All eggs in any one experiment were kept in the same way. Out of doors the pots were buried in the soil and in the laboratory they were usually kept in polythene bags. Specimen tubes containing eggs were stored in 8-inch high × 6-inch diameter aluminium cans lined with cotton wool.

Up to 11 per cent of the eggs were sterile and were removed when development had proceeded far enough for viable ones to be distinguished by the changing of their colour from white to cream, and by the pigmented mandibular sclerites of the embryo becoming visible through the chorion. Egg hatch was generally used as a criterion of diapause completion. Thus, in some experiments batches of diapausing eggs kept at different low temperatures were transferred at intervals to 20°C. for 12 days. Those which hatched were considered to have completed diapause. The effect of a particular low temperature treatment on rate of diapause development was shown by the proportion which hatched. In each treatment, 40–120 eggs were used. They were examined at 1–12 day intervals under a binocular stereoscopic microscope and egg hatch was determined by counting the empty egg shells. The hole through which the larva hatches is always just under the rim of the micropyle and is unmistakable because its inner edge is rasped away by the larval mandibules.

Experiments at constant temperatures of −20° C. to 30° C. were done in cabinets and rooms. The air temperature fluctuation in cabinets at 0° C. and −1° C. was within ± 0·2° C. In other rooms and cabinets it was within ± 1° C. except at −6, −12 and −20° C. where fluctuations of about ± 2° C. were recorded. However, the temperatures shown by thermometers inserted into pots of soil used for egg storage and into the specimen tubes within the aluminium cans remained constant when they were kept in a room at 20° C. ± 1° C. and in a cabinet at 7° C. ± 0·6° C. Therefore it is reasonable to assume that the temperature of the eggs was kept very constant at all temperatures except possibly in the rooms at −6, −12 and −20° C. where the air temperature fluctuations were relatively long term and may not have been suppressed entirely by the insulation around the eggs. The aluminium cans were lined with sheet lead when it was particularly important to keep temperature constant.

Thermographs were used for continuous temperature records. In outdoor experiments the bulbs of mercury-in-steel thermographs were buried beside the batches of eggs.

III. Egg Development in Natural Conditions

Eggs laid between 7th–15th of August were buried at depths of ¼ inch, 3 inches and 9 inches in bare soil. Temperature was recorded continuously at each depth and the egg hatch recorded at weekly intervals except when the

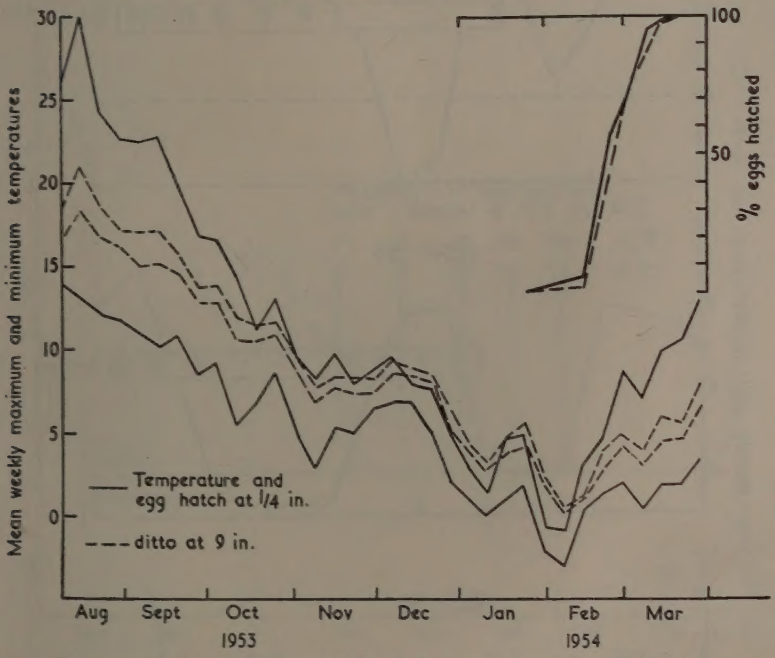

Fig. 1.—The cumulative percentage hatch of *L. coarctata* eggs in relation to the mean weekly maximum and minimum temperatures which they experienced at depths of ¼ inch and 9 inches in bare soil.

ground was frozen. The experiment was done for three successive years (1953–1956). Figure 1 shows the mean 7 day maxima and minima at ¼ inch and at 9 inches from August 1953 to March 1954. The temperature fluctuations from day to day and during each day were much greater at ¼ inch than at 9 inches, especially during the summer months. In August 1953, for example, the temperature extremes were 9·5° C. and 34·5° C. at ¼ inch and 15° C. and 20·5° C. at 9 inches. The average weekly temperature at 9 inches was higher than at ¼ inch but seldom by more than 1–1·5° C. Figure 1 shows that, despite these temperature differences, the eggs hatched at the same times.

Figure 2, A–C, shows when the eggs hatched in relation to the average temperature at ¼ inch for the three periods December–March, 1953–1956. Hatching began at the end of January but was not complete until mid-March.

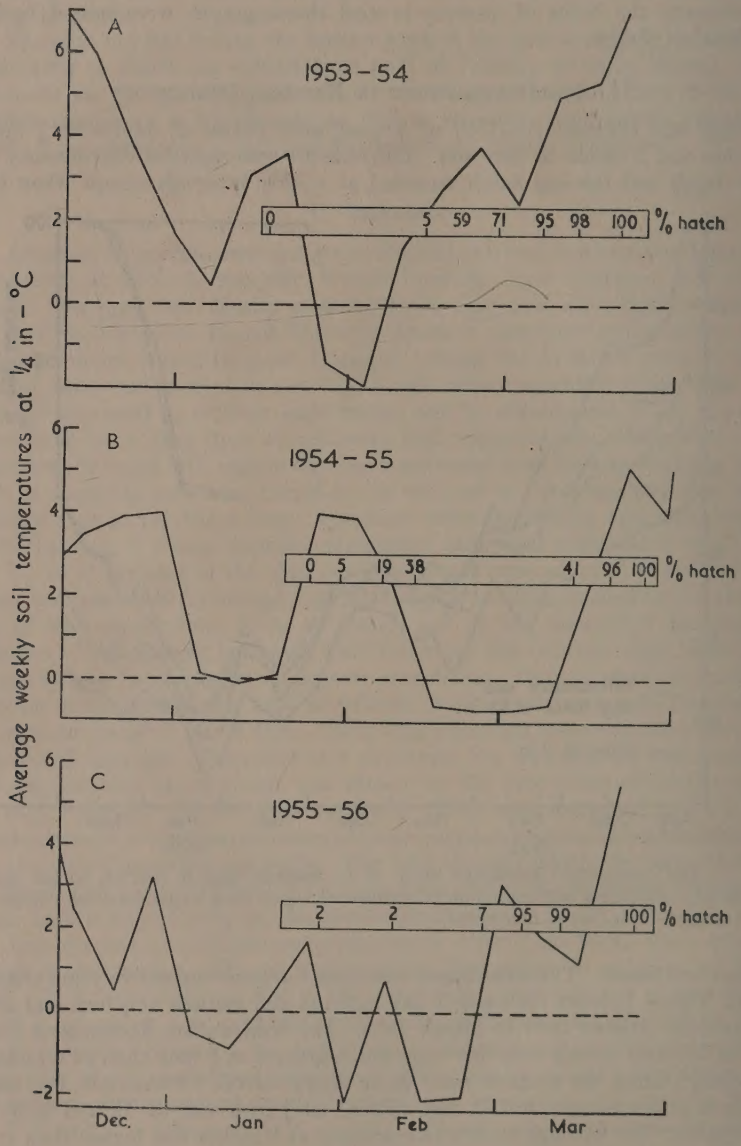

FIG. 2.—The cumulative percentage hatch of *L. coarctata* eggs in relation to average weekly soil temperatures at a depth of ¼ inch in bare soil in the years 1953–56.

Figure 2B shows that it stops when the temperature falls below 0° C., thus confirming Gough's (1946) conclusion that severe frosts delay hatching. Eggs seem able to hatch at, or just above, 0° C.

The above results suggest that, although all eggs had hatched in the field by mid-March, diapause development may have ended earlier. This suggestion was tested by removing batches of eggs to constant temperatures of 20° C. and 30° C. at intervals from mid-November. It will be shown later that diapause development is generally very slow or does not occur at above 20° C., and hence

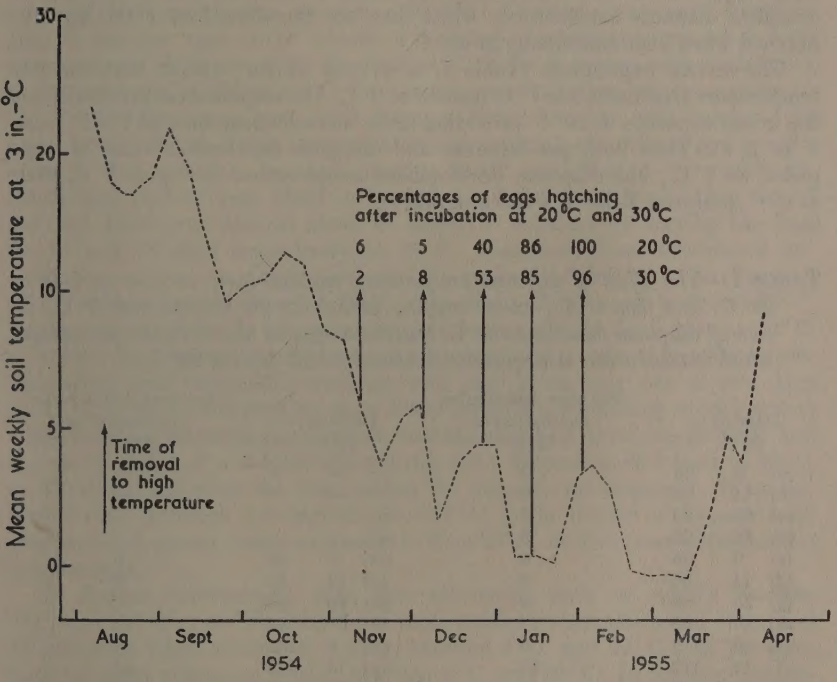

FIG. 3.—The time when diapause development terminated in eggs of *L. coarctata* as shown by the percentages hatching after being transferred at intervals to 20°C. and 30°C. The graph shows the average weekly soil temperature which the eggs experienced until they were transferred.

the proportion of eggs hatching within twelve days after transfer to such temperatures indicates the extent of earlier diapause development. Figure 3 shows that, in 1954–1955, diapause had ended in 2–6 per cent. of eggs by mid-November and in about 50 per cent. by the end of December. All eggs had completed diapause by the end of January, about 170 days after they were laid.

IV. Egg Development at Controlled Temperatures

Table I shows different temperature regimes in which eggs were kept from the time they were laid. In one experiment (Table I*a–l*) batches of eggs were

kept for 0, 14, 28 or 56 days at 20° C. followed by 0, 28, 56 or 112 days at 0° C., after which they were incubated at 20° C. for 12 days and the proportion which hatched recorded. Most hatched after 56 days at 20° C. followed by 112 days at 0° C. (Table I, *l*). It is significant that this treatment approximates to what the eggs experience in the field. No eggs hatched unless kept first at 20° C. (Table I, *a*, *e*, *i*). This is because 20° C., but not 0° C., is adequate for the pre-diapause morphological development. After about 14 days at 20° C. the embryo seems fully developed and has pigmented mandibular sclerites, although Table I, *j*, *k* and *l* show that a longer period at 20° C. is needed for the eggs to complete diapause satisfactorily when they are transferred to 0° C. No eggs hatched when kept continually at 20° C.

The second experiment (Table I, *m–u*) was similar, except that the low temperature treatment was 7° C. instead of 0° C. Development occurred without the initial exposure to 20° C. providing there was adequate time at 7° C. (Table I, *m*, *p*, *s*). Thus both pre-diapause and diapause development can be completed at 7° C., but diapause development seems rather slower at 7° C. than at 0° C. (*compare* Table I, *j* and *q*, *k* and *r*).

TABLE I.—*The effect of different temperature regimes* (a–l, *varying periods at* 20° *C. and then* 0° *C ;* m–u, *varying periods at* 20° C. *and then* 7° C.) *on rate of diapause completion in* L. coarctata *eggs as shown by the percentages which hatched when subsequently incubated for* 12 *days at* 20° *C.*

	Days at :— 20°C.	0°C.	Per cent. hatch after incubation at 20°C.		Days at :— 20°C.	7°C.	Per cent. hatch after incubation at 20°C.
(*a*)	0	28	0	—	—	—	—
(*b*)	14	28	0	—	—	—	—
(*c*)	28	28	2	—	—	—	—
(*d*)	56	28	5	—	—	—	—
(*e*)	0	56	0	(*m*)	0	56	0
(*f*)	14	56	0	(*n*)	14	56	0
(*g*)	28	56	0	(*o*)	28	56	0
(*h*)	56	56	17	—	—	—	—
(*i*)	0	112	0	(*p*)	0	112	43
(*j*)	14	112	56	(*q*)	14	112	45
(*k*)	28	112	73	(*r*)	28	112	53
(*l*)	56	112	96	—	—	—	—
—	—	—	—	(*s*)	0	196	76
—	—	—	—	(*t*)	14	196	97
—	—	—	—	(*u*)	28	196	94

The time needed for initial morphological development of the embryo at 20° C., about 14 days, is much longer than for non-diapausing eggs of related Diptera, such as *D. antiqua* Meig. (Miles, 1958). This suggests that diapause in the *L. coarctata* egg begins before morphological development is complete and gradually slows it down, finally stopping it. Therefore, although it is convenient to use the terms pre-diapause and diapause development, the one apparently merges into the other.

Table I, especially *j*, *k* and *l*, indicates that some diapause development can occur during the initial period at 20° C., which also seems adequate for the

final stages. Thus, out of a batch of 57 eggs kept at 7° C. for 16 weeks and then transferred to 20° C., 30 that had completed diapause at 7° C. hatched in less than 10 days, but 6 more hatched after an interval of 70–98 days. Presumably the six had completed the last part of their diapause development at 20° C. Similar results were obtained in other experiments in which a few of the eggs (8–16 per cent.), kept at a low temperature until diapause was almost complete, hatched 49–140 days after they were transferred to 20° C.

This evidence suggested that all stages of diapause development proceed at 20° C. but so slowly that the eggs die before diapause is complete, perhaps because their metabolites become exhausted. Experiments were therefore done to see how eggs in the middle of diapause development respond to high temperatures. Batches of 35–48, kept at 5° C. for 9 weeks, were transferred to temperatures of 20° to 40° C. for varying periods before returning them to 5° C. where they were kept until diapause ended and the eggs hatched. In figure 4 the numbers of eggs hatching at weekly intervals are given as percentages of those that survived, because viability varied according to the treatment. Provisional probits were fitted to the data and showed that the time for 50 per cent. hatch was delayed about 27 and 37 or 44 days by keeping the eggs for 14 and 28 days respectively at 20° C. Therefore, these treatments not only stopped but seemingly reversed the process of diapause development (*cf.* Schneiderman and Horwitz, 1958). The effects of exposures to 30 and 35° C. were more complex. In two separate experiments (fig. 4*a*, *b*), 7 days at 30° C. shortened the diapause development in a few eggs but prolonged it in the others. This effect was particularly striking with eggs given only one or two days at 30° C. or 35° C., where there was a sharp break in the hatching curve between those in which diapause development was shortened by about 40–50 days, and the rest in which it was little affected (fig. 4*a*). Exposures of 1 hour to 35° C. or 40° C. did not alter the time needed for diapause development. It is concluded that, although 1–7 days at 30 or 35° C. in the middle of diapause may shorten development, longer exposures to 20 or 30° C. stop, or reverse, the process in most eggs.

In further experiments, eggs were alternated daily or weekly between 5° C. and 20° C. or 30° C. Only 8 per cent. hatched when alternated daily, and 11 per cent. when alternated weekly, between 5° C. and 20° C.; 24 per cent. hatched when alternated weekly between 5° C. and 30° C. In the same experiment, 89 per cent. and 0 per cent. of eggs hatched when kept continuously at 5° C. and 20° C. respectively.

V. Optimum Constant Temperature for Diapause Development

Eggs laid on three successive days were kept outdoors 3 inches deep in soil for 65–68 days after they were laid. By then pre-diapause development was complete and diapause had begun. Batches were then transferred to each of ten constant temperatures between —20 and 16° C. Eggs given temperatures below freezing were conditioned for 3 days at 0° C. followed where necessary by 3 days at —6° C. After 56[1], 77, 98 and 119 days, 40–60 eggs were removed from each treatment and incubated at 20° C. The extent of diapause develop-

[1] Eggs at —20, —12 and —6°C. were in error given 59 days instead of 56 days.

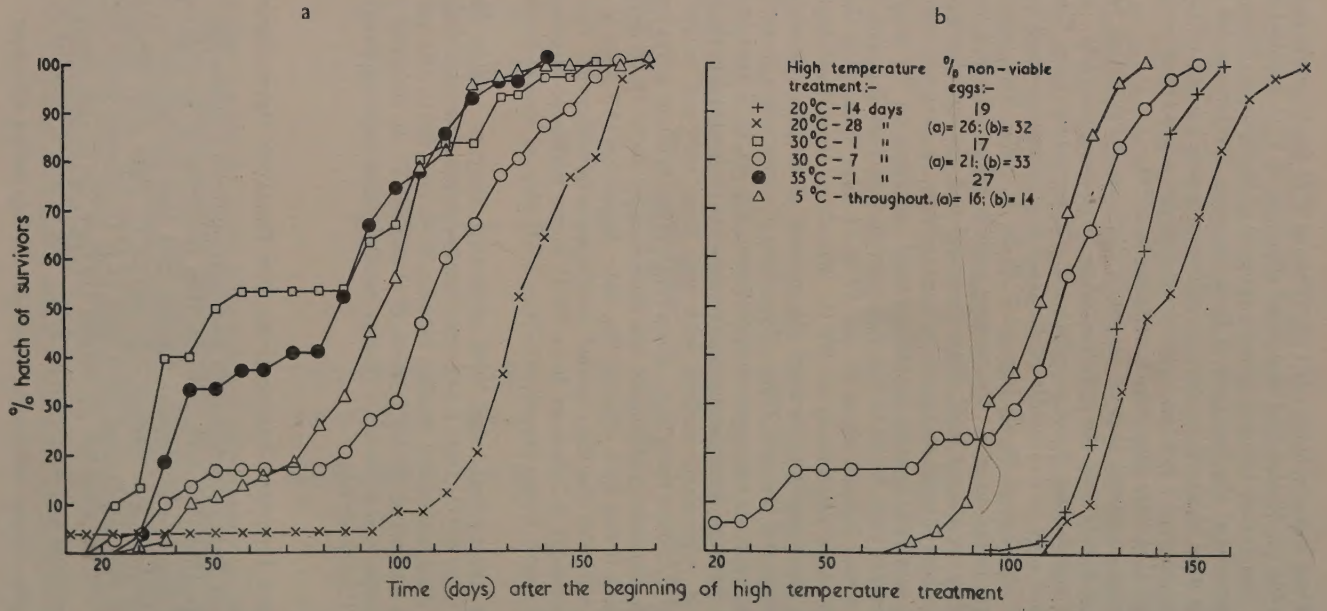
a
b
% hatch of survivors
Time (days) after the beginning of high temperature treatment
High temperature treatment:-
% non-viable eggs:-
20°C - 14 days 19
20°C - 28 " (a)= 26; (b)= 32
30°C - 1 " 17
30°C - 7 " (a)= 21; (b)= 33
35°C - 1 " 27
5°C - throughout. (a)= 16; (b)= 14

FIG. 4.—Graphs showing how the duration of diapause in eggs of *L. coarctata* was affected by short periods at high temperatures in the middle of diapause development at 5°C.

ment in each treatment, as indicated by the percentage of eggs that hatched, is shown graphically in figure 5. After 56 days, diapause development was complete in 51 per cent. of eggs kept at —20° C., in 6 per cent. kept at —6° C., in 52 per cent. at 1° C. and in none at 12° C. Except at —20 and latterly at 12° C. the proportions hatching increased with longer exposure to the low temperature.

Similar results were obtained in another experiment where the newly laid eggs were kept at 20° C., instead of outdoors, for pre-diapause development.

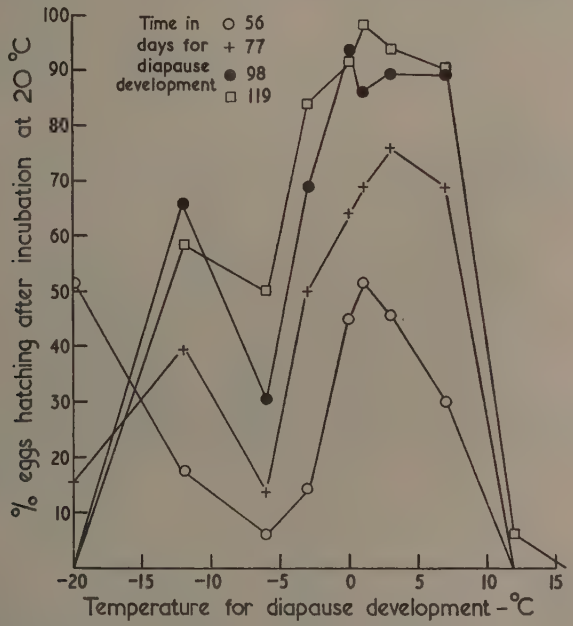

FIG. 5.—The percentages of *L. coarctata* eggs which hatched when incubated at 20°C. after being kept during diapause at temperatures varying from —20°C. to 16°C. for 56 to 119 days.

Provisional probits (Finney, 1952) were fitted to both sets of data, and the rates of diapause development at each temperature

$$\frac{100}{\text{Time in days for 50 per cent. hatch}}$$

are shown graphically in figure 6. Diapause development was most rapid at a constant temperature of 3° C., when it was about twice as fast as at —6° C., but only about one and a half times faster than at —12° C. This suggests that there may be two peaks in the curve for rate of diapause development, one at about 3° C. and the other below —12° C. The upper limit for satisfactory diapause development is between 7° C. and 12° C.

VI. Development Before and After Diapause

As mentioned already, the end of pre-diapause morphological development seems to merge into the beginning of diapause development, although it is evident that they have different temperature requirements. The following experiments show the temperature limits for pre-diapause development. A

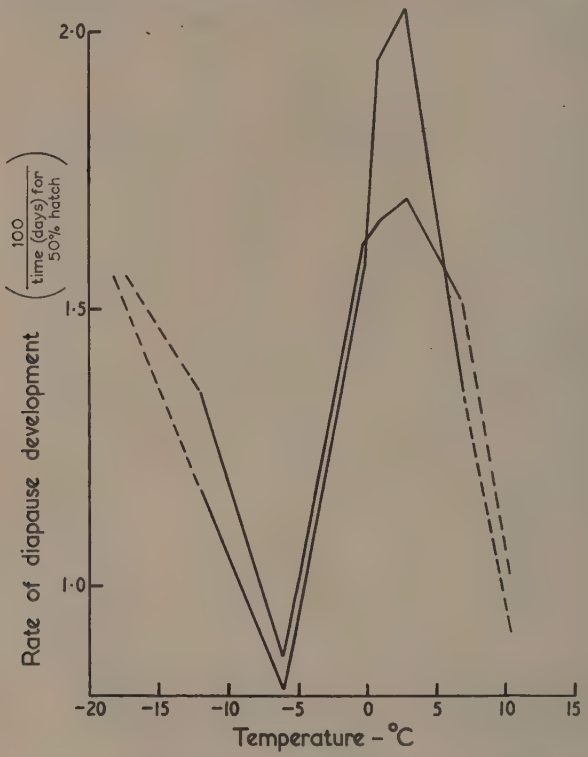

Fig. 6.—Graph based on results of two experiments showing the effect of temperature on the rate of diapause development in eggs of *L. coarctata*.

batch of newly hatched eggs was kept 21 days at 30° C. for pre-diapause development and then given 180 days at 0° C. for diapause development; 88 per cent. hatched after incubation at 20° C. Further, 83 per cent. hatched when kept at 3° C. from the time they were laid. Table I*i* shows that 0° C. is too low for pre-diapause development and this was confirmed by observations that the embryo did not develop morphologically at this temperature. Therefore the lower threshold for pre-diapause development is between 0° C. and 3° C. and the upper is above 30° C.

Figure 3 shows that post-diapause development is completed satisfactorily at 30° C., whereas figure 2 suggests that it may occur also at temperatures

down to 0° C. To test this, eggs that had completed diapause development at −3° C. were kept at 0° C., −1° C. and −3° C. After 129 days 92 per cent. had hatched at 0° C. and none at −1° C. and −3° C. Water in the chorion froze at −1 and −3° C.; to test whether hatching would occur were freezing prevented, some eggs were dipped in 5 per cent. glycerol in water at the beginning of the experiment, but they did not hatch. Post-diapause development is therefore possible within the range 0° C. to over 30° C.

The duration of post-diapause development at 20° C. was determined using eggs previously kept at 0° C., −3°C. or −12° C. until diapause was complete. Table II shows that no eggs hatched after one day's incubation at 20° C. but over 90 per cent. did after 5–9 days. Eggs kept previously at −12° C. took about 2 days longer to hatch than the others.

TABLE II.—*Duration of post-diapause development of* L. coarctata *at* 20° *C. as shown by the cumulative percentage hatch of eggs which has completed diapause at temperatures of* 0, −3 *and* −12° *C.*

Temperature for diapause development	No. of days after transfer to 20°C.					
	1	3	5	7	9	11
0°C.	0	43	93	97	100	—
−3°C.	0	41	96	100	—	—
−12°C.	0	11	59	85	96	100

It seems that little morphogenesis can occur during the short phase of post-diapause development, especially as part of the time is needed both for physiological changes that reactivate the embryo (Van der Kloot, 1955) and for the process of hatching.

VII. Development at Constant Temperatures

The above experiments show that the temperature requirements for all stages of development overlap in the range 3° C. to 12° C., although the latter is too high for satisfactory diapause development (*see* fig. 5). However, some eggs should be able to develop from laying to hatching at any constant temperature within these limits. Results of experiments to test this are given in figure 7 and Table III. Figure 7 shows that development was quickest and most eggs hatched at 7° C., probably because it is midway between the threshold of every stage of development, whereas 3° C. is close to the minimum threshold for pre-diapause development and 12° C. is beyond the upper limit of satisfactory diapause development.

TABLE III.—*The percentages of eggs of* L. coarctata *which hatched when kept at constant temperatures from the time they were laid*

	Constant temperature °C.					
	0	3	7	10	12	16
Per cent. hatch	0[1]	87	95	68[1]	32	0

[1] Separate experiment from that done at the other temperatures.

VIII. Discussion

The temperature requirements for development of the *L. coarctata* egg show how well it is adapted to its environment. Relatively high temperatures from August to mid-October are more than adequate for pre-diapause development. This long initial exposure to relatively high temperatures does not intensify the subsequent diapause as in some insect eggs (Andrewartha, 1943; Muroga, 1951; Browning, 1952) but seemingly shortens it (*cf.* LeBerre, 1953).

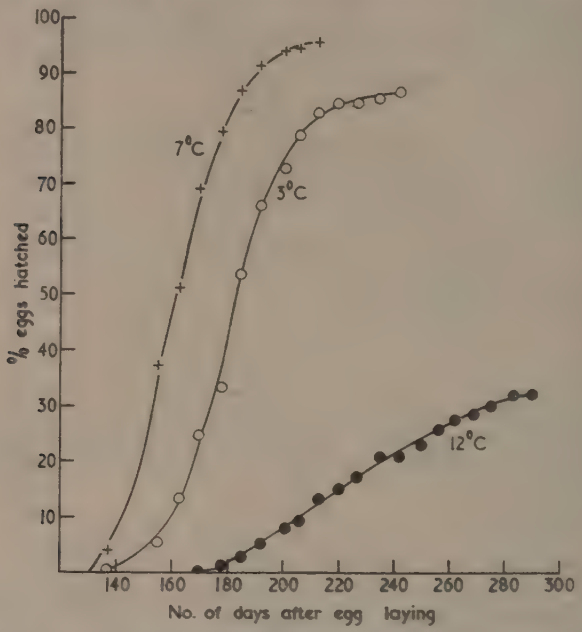

Fig. 7.—Rate of hatch of *L. coarctata* eggs kept at constant temperatures of 3°C., 7°C. and 12°C. from the time they were laid.

The weekly average soil temperatures after mid-October are within ± 4° C. of the optimum constant temperature for diapause development which always ends by the end of January. Temperatures down to 0° C. do not stop post-diapause development, so the larva can hatch early in the year.

Diapause development occurs satisfactorily at constant temperatures in the range −6 to about 10° C., with the optimum about 3° C. It cannot be assumed, however, that this temperature is best for all stages of diapause, and evidence that in some eggs the early and late stages can proceed at 20° C. (Table I) suggests that the optimum temperature may change as diapause proceeds, corresponding with the changing environmental temperature.

The shortening of diapause development in some eggs by exposing them for 1–7 days to 30° C. and 35° C. is not ecologically significant because these temperatures do not occur naturally during autumn and winter. The action

appears to be like that of the high temperature shock treatments that break diapause in some other insects (Roubaud, 1922 ; Emme, 1946) ; it also resembles the effect of high temperatures at the end of diapause in *Cephus cinctus* Nort., when two days of high temperature accelerate post-diapause development, whereas longer periods reinstate diapause (Salt, 1947 ; Church, 1955).

Soil temperatures in Britain seldom fall below about —5° C. ; hence the egg of *L. coarctata* does not benefit from being able to complete diapause at below —12° C. This, however, is interesting because it indicates that physiological reactions that end diapause can proceed at temperatures below the threshold at which usual biochemical reactions can be detected. It is discussed separately (Way, *in press*).

IX. Summary

The eggs of *L. coarctata* Fallén are usually laid on bare soil in August and hatch during the following January–March.

The embryo apparently becomes fully developed during pre-diapause morphological development which merges imperceptibly into the diapause stage. Diapause ends by January, and the eggs begin to hatch shortly afterwards when the temperature is above 0° C.

Although eggs near the surface experienced much greater temperature fluctuations than those deeper in the soil, all hatched at the same time.

Within the normal temperature range, the lower and upper limits for the different stages of development are : — pre-diapause morphological development—between 0–3° C. and over 30° C. ; diapause physiological development —6° C. and 12° C.; post-diapause development (reactivation and hatching)— 0° C. and over 30° C. The optimum constant temperature for diapause development is about 3° C. The egg can develop through all stages at constant temperatures between 3° C. and 12° C.; the optimum is about 7° C. Development is accelerated in some eggs by transferring them in the middle of their diapause to 30° C. or 35° C., for 1–7 days, but it is stopped or reversed by an interval of 2–4 weeks at 20° C.

Development can proceed at the beginning of diapause, and to a lesser extent towards the end, at a temperature above the upper limit for the intervening stages. This suggests that the temperature optimum for diapause may vary as development proceeds.

Diapause development at —20° C. may be as fast as at 3° C. This is not ecologically significant but may help towards understanding the physiology of diapause.

X. Acknowledgments

I am grateful to the Low Temperature Research Station, Cambridge, for providing constant temperature facilities.

XI. References

Andrewartha, H. G., 1943, Diapause in the eggs of *Austroicetes cruciata*, Sauss. (Acrididae) with particular reference to the influence of temperature on the elimination of diapause. *Bull. ent. Res.* **34** : 1–17.

—— 1952, Diapause in relation to the ecology of insects. *Biol. Rev.* **27** : 50–107.

Bardner, R. and Kenten, J., 1957, Notes on the laboratory rearing and biology of the wheat bulb fly, *Leptohylemyia coarctata* (Fall.). *Bull. ent. Res.* **48** : 821–831.

Browning, T. O., 1952, The influence of temperature on the completion of diapause in the eggs of *Gryllulus commodus* Walker. *Aust. J. Sci. Res.* (B) **5** : 112–127.

Church, N. S., 1955, Hormones and the termination and reinduction of diapause in *Cephus cinctus* Nort. (Hymenoptera : Cephidae). *Canad. J. Zool.* **33** : 339–369.

Danilyevsky, A. S., 1949, The dependence of the geographical distribution of insects on the ecological peculiarities of their life cycles. [In Russian]. *Ent. Oboz.* **30** : 194–207.

Emme, A. M., 1946, Removal of embryonic diapause in *Bombyx mori* L. by applying sub-lethal thermal treatment. Variation in sensitivity of graine. *C.R. Acad. Sci. URSS* (*N.S.*). **52** : 645–648.

Finney, D. J., 1952, *Probit analysis. A statistical treatment of the sigmoid response curve.* 2nd. ed. Cambridge University Press.

Gough, H. C., 1946, Studies on Wheat Bulb Fly (*Leptohylemyia coarctata* Fall.). I. Biology. *Bull. ent. Res.* **37** : 251–271.

Hodson, A. C. and Weinman, C. J., 1945, Factors affecting recovery from diapause and hatching of eggs of the Forest Tent Caterpillar, *Malacosoma disstria* Hbn. *Tech. Bull. Minn. Agric. Exp. Sta.* No. 170.

LeBerre, J. R., 1953, Contribution a l'étude biologique du criquet migrateur des Landes (*Locusta migratoria gallica* Remaudière). *Bull. biol.* **87** : 227–273.

Lees, A. D., 1953, Environmental factors controlling the evocation and termination of diapause in the fruit tree red spider mite (*Metatetranychus ulmi* Koch (Acarina : Tetranychidae)). *Ann. appl. Biol.* **40** : 449–486.

—— 1955, *The physiology of diapause in Arthropods.* Cambridge University Press.

Miles, M., 1958, Studies of British Anthomyid flies. IX. Biology of the Onion Fly, *Delia antiqua* (MG.). *Bull. ent. Res.* **49** : 405–414.

Muroga, H., 1951, On the consumption coefficient of inhibitory substance in silkworm eggs. [In Japanese, English title]. *J. Seric. Sci. Japan* **20** : 92–94.

Prebble, M. L., 1941, The diapause and related phenomena in *Gilpinia polytoma* (Hartig). II. Factors influencing the breaking of diapause. *Canad. J. Res.* (D) **19** : 323–346.

Roubaud, E., 1922, Sommeil d'hiver cédent à l'hiver chez les larves et nymphes des Muscides. *C.R. Acad. Sci., Paris* **174** : 964–975.

Salt, R. W., 1947, Some effects of temperature on the production and elimination of diapause in the Wheat Stem Sawfly, *Cephus cinctus* Nort. *Canad. J. Res.* (D) **25** : 66–86.

Schneiderman, H. A. and Horwitz, J., 1958, The induction and termination of facultative diapause in the Chalcid wasps *Mormoniella vitripennis* (Walker) and *Tritneptis klugii* (Ratzeburg). *J. exp. Biol.* **35** : 520–551.

Van der Kloot, W. G., 1955, The control of neurosecretion and diapause by physiological changes in the brain of the *Cecropia* silkworm. *Biol. Bull.* **109** : 276–294.

Way, M. J. (*in press*), The effects of freezing temperatures on the developing egg of *Leptohylemyia coarctata* with special reference to the mechanism of diapause development. *J. Ins. Physiol.*

Williams, C. M., 1956, Physiology of insect diapause. X. An endocrine mechanism for the influence of temperature on the diapausing pupa of the *Cecropia* silkworm. *Biol. Bull.* **110** : 201–218.